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The need for long-term ecological research in subterranean environments

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Abstract. Subterranean habitats, those found beneath the surface of nonmarine environments such as caves, aquifers, and other underground voids, are more widespread and ecologically significant than often assumed. These environments are functionally linked to the adjacent surface ecosystems, sharing hydrological, geochemical, and biological connections. Despite their global distribution and ecological importance, subterranean habitats remain among the least-explored and least-understood ecosystems. However, the scientific neglect of these environments is not limited to species inventories or basic ecological descriptions. This note highlights the near-complete absence of long-term ecological research (LTER) conducted on subterranean ecosystems. While LTER programmes are increasingly recognized as essential for understanding ecosystem dynamics, biodiversity trends, and the impacts of environmental change in terrestrial, freshwater, and marine systems, this kind of study appears to be extremely rare in subterranean environments. The lack of reference long-term studies hinders our ability to detect and interpret temporal changes in community composition, species interactions, and evolutionary processes within these unique environments. Nevertheless, there are compelling scientific reasons to promote the development of long-term ecological research in subterranean ecosystems. In fact, these simplified and relatively buffered habitats offer unique opportunities to study community interactions and adaptations under relatively stable climatic conditions. Furthermore, subterranean environments may serve as natural laboratories for investigating evolutionary processes such as ecological adaptation, morphological convergence, speciation and gene flow, especially when compared to the more variable surface environments with which they are functionally linked.

Keywords: biodiversity, caves, climate change, ecological change, underground ecosystems, long-term study.

1. Introduction

1.1. Subterranean habitats

In recent years, there has been a growing interest in the ecology, evolution, and conservation of cave habitats and, in general in subterranean or underground ecosystems (e.g., Culver & Pipan, 2009, 2014; Mammola et al., 2019a, b, 2024; Mata da Rocha Melo et al., 2025; Niemiller et al., 2025). The scientific interest in these systems reflects a broader recognition of their biodiversity uniqueness, their role in global ecological processes, and the threats they face in the Anthropocene (Mammola et al., 2019a, b; Saccò et al., 2023).

Contrary to common opinion, subterranean habitats are far more widespread than typically perceived. Indeed, they are found beneath the surface of approximately 19% of the Earth's nonmarine environments (Mammola et al., 2019b; Sánchez-Fernández et al., 2021). These environments are diverse ranging from limestone karstic systems and lava tubes to shallow superficial habitats and man-made structures such as tunnels and mines (White et al., 2019; Culver & Pipan, 2014; Mammola et al., 2024). Subterranean habitats are functionally connected to the surrounding surface ecosystems through continuous hydrological, geochemical and biological exchanges (e.g., Luis-Vargas et al., 2024), while possessing divergent environmental conditions. One of the most significant characteristics of subterranean environments is the absence of sun irradiation: light is reduced near the entrance and completely absent in deeper areas (White et al., 2019; Culver & Pipan, 2009). As a result, these ecosystems lack photoautotroph organisms and rely heavily on allochthonous inputs of organic material from the surface. Nutrients and organic subsidies are introduced through water percolation, air currents, and the seasonal or daily movements of animals between terrestrial and subterranean habitats (Trajano, 2000; Culver & Pipan, 2009; Simon et al., 2007; Mammola et al., 2019a). The microclimate in subterranean habitats is highly constant, with reduced variations, due to the isolation from atmospheric fluctuations provided by geological substrate. Moreover, these habitats exhibit a high degree of thermal inertia i.e., the capacity to delay the effects of changes in temperature in relation to external climatic fluctuations (Domínguez-Villar et al., 2015). This feature makes subterranean systems relatively buffered from short-term environmental variations and contributes to their status of climate-stable refugia in the face of global climate change (Domínguez-Villar et al., 2015). However, this same thermal inertia also means that subterranean-adapted species tend to have low physiological plasticity and are particularly vulnerable to even slight alterations in their environmental conditions, such as temperature and air humidity (e.g., Raschmanová et al., 2018; Mammola et al., 2019b). In addition, the biological communities inhabiting subterranean ecosystems are often simplified compared to surface ecosystems, in part due to the absence of light and photosynthetic organisms (Poulson & White, 1969; Culver & Pipan, 2009; 2014). These conditions impose strong selective pressures on resident organisms, leading to the evolution of highly specialized ecological adaptations. Subterranean animals, often referred to as troglobionts (Sket, 2008), typically display morphological and physiological adaptations such as loss of pigmentation, eye reduction, elongation of appendages, and enhanced non-visual sensory mechanisms (Poulson & White, 1969; Pipan et al., 2010; Mammola et al., 2019b). Therefore, subterranean species frequently exhibit narrow geographic ranges, often limited to single caves or unique karst systems (Ficetola et al., 2019). The restricted distribution of cave-adapted organisms, combined with their highly specialized ecological niches and low dispersal capabilities, increase the risk of local and global extinctions of entire cave communities when their habitats are disturbed or modified by human activities, such as water extraction, pollution, mining and introduction of invasive allochthonous species (Mammola et al., 2022).

Despite these challenges, subterranean ecosystems hold great scientific value for better understanding evolutionary and ecological processes (e.g., Ficetola et al., 2019; Mammola et al., 2021). The relative isolation and environmental constancy of subterranean physical conditions make these habitats natural laboratories for studying species interactions, convergent evolution, genetic drift, and speciation mechanisms (Culver & Pipan, 2014; Ficetola et al., 2019). In fact, these environments offer unique opportunities to examine how species evolve in response to extreme but stable conditions, providing insights that are relevant to broader and unresolved questions in evolutionary biology, ecological dynamics and conservation genetics (Poulson & White, 1969; Mammola et al., 2020; Luis-Vargas et al., 2024).

1.2. Relevance of long-term ecological research

The scientific value of long-term ecological research in investigating evolutionary and ecological change, complex biological interactions, and the impacts of rare or extreme climatic events on biological communities is well recognized (e.g., Likens, 1989; Jones and Driscoll, 2022; Blanc & Thrall, 2024; Stroud & Ratcliff, 2025). This kind of research provides insights that cannot be obtained from short-term studies, because many ecological and evolutionary processes unfold only over extended periods (Reinke et al., 2019; Stroud & Ratcliff, 2025). While long-term ecological research can be defined in multiple ways, for the purposes of this note we follow the relatively vague but practical definition proposed by Lindenmayer et al. (2013): long-term ecological studies are those that involve the systematic and regular collection of field data from a specific site, population or community over an extended period (more than a decade, according to the original paper of Lindenmayer et al., 2013). This criterion emphasizes not only the duration but also the methodological consistency of the sampling technique used to obtain field data from the focal system. These two aspects are essential for separating gradual and persistent ecological trends from short-term variability and for capturing rare, unexpected but influential environmental events. Indeed, long-term ecological research allows a deeper understanding of evolutionary and ecological processes that occur over long periods of time (Reinke et al., 2019; Stroud & Ratcliff, 2025). As an example, this research approach seems fundamental for better understanding evolutionary dynamics, ecological interactions, and adaptative responses of biological populations and entire communities to ongoing climatic events (e.g., Jones & Driscoll, 2022).

National and international scientific institutions acknowledge the importance of systematically and regularly recording ecological data from different ecosystems. To this end, the Long-Term Ecological Research (LTER) international network was established to better understand ecological processes such as state change, resilience and cascading effects in a variety of terrestrial, freshwater and marine environments over different biogeographic regions around the globe (e.g., Rastetter al., 2021).

2. Goal of the study

In this note we highlight the lack of long-term research projects specifically focusing on ecological and evolutionary questions taking place in subterranean environments. To address this question, we checked the international LTER website to find research projects dealing with the ecology of subterranean environments or communities. Moreover, we searched the Scopus scientific database with the goal of retrieving papers with "long-term ecological research" in the title, abstract and keywords. In subsequent queries the habitat type was added with the option "and", while in the case of multiple similar habitats they were subsequent added with the option "or" (i.e., "sea" or "ocean" or "marine"). Results from these queries should be considered as preliminary efforts to drive attention on the highly skewed distribution of long-term ecological research publications in different environments, suggesting an evident underrepresentation of studies in subterranean habitats, specifically when compared to all other marine, freshwater and terrestrial habitats. In this research note, we draw attention on the fact that lack of scientific research extends beyond basic descriptions of subterranean biodiversity but is also affects long-term ecological studies.

3. Long-term ecological research in the subterranean environment

Long-term field studies were apparently not homogeneously distributed among different ecological environments and ecosystems. For instance, there were no subterranean research sites listed on the LTER international website (https://www.ilter.network/), consulted in March 2025.

Overall, 1491 scientific papers dealing with "long-term ecological research" were retrieved from the Scopus database (Fig. 1). The distribution of scientific publications citing in their title, abstract or keywords the sentence "long-term ecological research" shows a huge variation, according to the habitat considered (Fig. 1). Only four out of 1491 (3‰) scientific publications were devoted to subterranean habitats, ecosystems or species. However, these results should not be considered to be completely comprehensive, because scientific papers could overlap over different categories and some long-term studies may have been overlooked by our simplified searching procedure.

4. The need for more research in subterranean environments

The insignificant proportion of long-term research dealing with the ecology, evolution or conservation of biodiversity in subterranean environments is astonishing. Our preliminary observations underscore how subterranean ecosystems remain largely neglected from both the ecological and evolutionary perspective, in addition to previous reports (Ficetola et al., 2019; Mammola et al., 2019a; Mata da Rocha

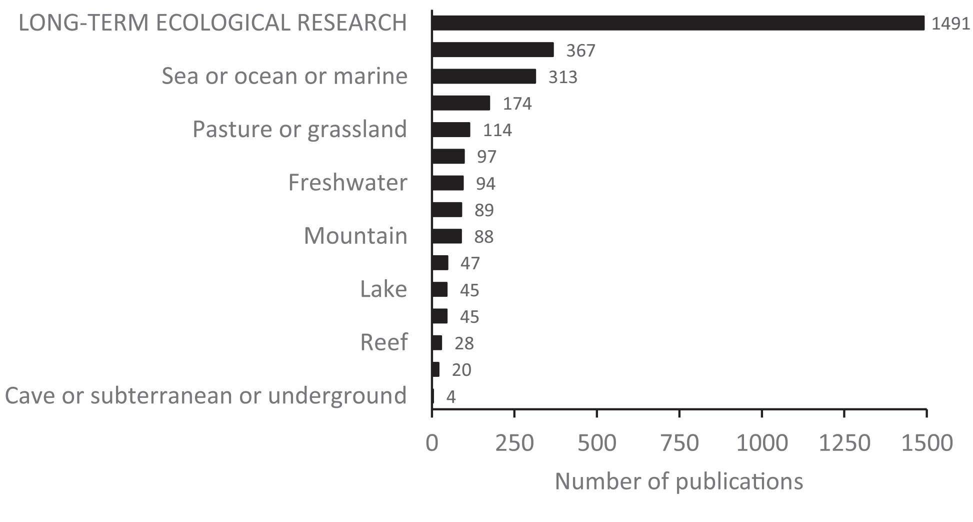

Figure 1. Distribution of scientific publications over different environments or habitats retrieved from Scopus database on March 19th, 2025

Melo et al., 2025; Silveira, 2025). This because subterranean environments are, together with deep seafloors, among the less explored, mapped and basically described ecosystems (Culver et al., 2012; Ficetola et al., 2019). There are objective difficulties in accessing such extreme environments and, usually, permanent subterranean laboratories are conceived to investigate physics, astrophysics, geophysics or the influence of reduced radioactivity on biological organisms (Bettini, 2011; Ianni, 2021).

Furthermore, subterranean ecosystems seem also absent from future climate change agendas (Sánchez-Fernández et al., 2021) and have not been taken into consideration in the recent European Green Deal policy (Fišer et al., 2022), while hosting species and communities of high conservation concern (Vaccarelli et al., 2023; Sánchez-Fernández et al., 2021). These considerations raise concern about the need of future conservation and management policies concerning these widespread but understudied ecosystems (Fišer et al., 2024; Silveira, 2025). However, even if subterranean habitats seem relatively buffered in relation to external climatic variation, their biological communities could be extremely sensible to limited and short-term variations of their physical characteristics (e.g., Mammola et al., 2019b; Sánchez-Fernández et al., 2021) or to the ecological impact of recently introduced invasive species (Nicolosi & Gerovasileiou, 2024; Nicolosi et al., 2023). In any case, subterranean habitats offer ideal settings for testing ecological and evolutionary theories, as they present well identifiable microclimatic gradients while hosting relatively simplified biological communities (e.g., Mammola, 2019; Sánchez-Fernández et al., 2018).

The need for long-term ecological research for monitoring changes in distribution and abundance of biological communities and their temporal trends has been supported before (e.g., Ficetola et al., 2019; Mammola et al., 2020). Here we stress again this concept, extending the issue to long-term studies on subterranean biodiversity. In fact, it would be valuable to increase the number of subterranean long-term research projects establishing and developing them in proximity of experimental superficial sites in which already ongoing such projects are already active. Tracking at the same time energy flows, biodiversity, ecological interactions, invasive species and climate change effects between adjacent and functionally linked ecosystems will provide new insights on the pace and the mechanisms of ecological and evolutionary change in these different environments. Therefore, establishing reference subterranean sites in which the variations over time in the spatial niche, occupancy, abundance and ecological interactions among species should be encouraged and possibly funded by national and international institutions. These long-term research projects should be especially attractive for ecologists and evolutionary biologists interested in understanding the different ecological dynamics occurring across adjacent and functionally linked superficial and subterranean environments.

Declaration of interest statement

The authors declare that they have no conflicts of interest. AC was partially supported by UNIGE FRA2022-23 and FRA2023-24 fundings. LLMs have been used to polish the English.

References

Bettini, A., 2011, Underground laboratories. Nuclear Instruments and Methods in Physics Research A 626–627: S64–S68.

Blanc, S., & Thrall, P.H., 2024, The critical role of very long-term studies in ecology and evolution. Ecology Letters 27, e70049.

Culver, D.C., & Pipan, T., 2009, The biology of caves and other subterranean habitats. Oxford, Oxford University Press.

Culver, D.C., Trontelj, T., Zagmajster M., & Pipan, T., 2012, Paving the way for standardized and comparable subterranean biodiversity studies. Subterranean Biology 10: 43–50. doi: 10.3897/subtbiol.10.4759

Culver, D.C, & Pipan, T., 2014, Shallow sub terranean habitats: ecology, evolution and conservation. Oxford, Oxford University Press.

Domínguez-Villar, D., Loje, S., Krklec, K., Baker, A., & Fairchild,I.J., 2015, Is global warming affecting cave temperatures? Experimental and model data from a paradigmatic case study. Climate Dynamics 45: 569–581.

Ficetola, G.F., Canedoli, C., & Stoch, F., 2019, The Racovitzan impediment and the hidden biodiversity of unexplored environments. Conservation Biology 33: 214–216.

Fišer, C., Borko, S., Delic, T., Kos, A., Premate, E., Zagmajster, M., Zakšek, V., & Altermatt, F., 2022, The European green deal misses Europe's subterranean biodiversity hotspots. Nature Ecology & Evolution 6: 1403–1404.

Ianni, A., 2021, Science in underground laboratories and DULIA-Bio. Frontiers in Physics 9, 612417.

Jones, J.A., & Driscoll, C.T., 2022, Long-term ecological research on ecosystem responses to climate change. BioScience 72(9): 814–826.

Likens, G.E., 1989, Long-term studies in ecology. Approaches and alternatives. Springer Verlag, New York.

Lindenmayer, D.B., Liken, G.E., Andersen, A., Bowman, D., Bull, C.M., Burns, E., Dickman, C.R., Hoffmann, A.A., Keith, D.A., Liddell, M.J, Lowe, A.J., Metcalfe, D.J, Phinn, S.R., Russell-Smith, J., Thurgate, N., & Wardle, G.M., 2012, Value of long-term ecological studies. Austral Ecology 37: 745–757.

Luis-Vargas, M.N., Webb, J., & Bay, S.K., 2024, Linking surface and subsurface: The biogeochemical basis of cave microbial ecosystem services. Journal of Sustainable Agriculture and Environment 3, e70031.

Mammola, S., 2019, Finding answers in the dark: caves as models in ecology fifty years after Poulson and White. Ecography 7: 1331–1351.

Mammola, S., Altermatt, F., Alther, R., Amorim, I.R., Băncilă, R.I., Borges, P.A.V., Brad, T., Brankovits, D., Cardoso, P., Cerasoli, F., Chauveau, C.A., Delić, T., Di Lorenzo, T., Faille, A., Fišer, C., Flot, J-P., Gabriel, R., Galassi, D.M.P., Garzoli, L., Griebler, K., Konecny-Dupré, L., Martínez, A., Mori, N., Nanni, V., Ogorelec, Z., Pallarés, S., Salussolia, A., Saccò, M., Stoch, F., Vaccarelli, I., Zagmajster, M., Zittra, C., Meierhofer, M.B., Sánchez-Fernández, D., & Malard, F., 2024, Perspectives and pitfalls in preserving subterranean biodiversity through protected areas. NPJ Biodiversity 16, 2.

Mammola, S., Amorim, I.R., Bichuette, M.E., Borges, P.A., Cheeptham, N., Cooper, S.J., Culver, D.C., Deharveng, L., Eme, D., Ferreira, R.L., Fišer, C., Fišer, Ž, Fong, D.W., Griebler, C., Jeffery, W.R., Jugovic, J., Kowalko, J.E., Lilley, T.M., Malard, F., & Cardoso, P., 2020, Fundamental research questions in subterranean biology. Biological Reviews 95: 1855–1872.

Mammola, S., Cardoso, P., Culver, D.C., Deharveng, L., Ferreira, R.L., Fišer, C., Galassi, D.M.P., Griebler, C., Halse, S., Humphreys, W.F., Isaia, M., Malard, F., Martinez, A., Moldovan, O.T., Niemiller, M.L., Pavlek, M., Reboliera, A.S.P.S., Sousa-Silva, M., Teeling, E.C., Wynne, J.J., & Zagmajster, M., 2019a, Scientists' warning on the conservation of subterranean ecosystems. Bioscience 69: 641–650.

Mammola, S., Lunghi, E., Bilandžija, H., Cardoso, P., Grimm, V., Schmidt, S., Hesselberg, T., & Martinez, A., 2021, Collecting eco-evolutionary data in the dark: Impediments to subterranean research and how to overcome them. Ecology and Evolution 11: 5911–5926.

Mammola, S., Meierhofer, M.B., Borges, P.A.V., Colado, R., Culver, D.C., Deharveng, L., Delić, T., Di Lorenzo, T., Dražina, T., Ferreira, R.L., Fiasca, B., Fišer, C., Galassi, D.M.P., Garzoli, L., Gerovasileiou, V., Griebler, C., Halse, S., Howarth, F.G., Isaia, M., Johnson, J.S., Komerički, A., Martínez, A., Milano, F., Moldovan, O.T., Nanni, V., Nicolosi, G., Niemiller, M.L., Pallarés, S., Pavlek, M., Piano, E., Pipan, T., Sanchez-Fernandez, D., Santangeli, A., Schmidt, S.I., Wynne, J.J., Zagmajster, M., Zakšek, V., & Cardoso, P., 2022, Towards evidence-based conservation of subterranean ecosystems. Biological Review of the Cambridge Philosophical Society 97: 1476–1510. doi: 10.1111/brv.12851

Mammola, S., Piano, E., Cardoso, P., Vernon, P., Domínguez-Villar, D., Culver, D.C., Pipan, T., & Isaia, M., 2019b, Climate change going deep: The effects of global climatic alterations on cave ecosystems. Anthropocene Review 6: 98–116.

Mammola, S., Altermatt, F., Alther, R., Amorim, I.R., Băncilă, R.I., Borges, P.A., Brad, T., Brankovits, D., Cardoso, P., Cerasoli, F., Chauveau, C.A., Delić, T., Di Lorenzo, T., Faille, A., Fišer, C., Flot, J.F., Gabriel, R., Galassi, D.M.P., Garzoli, L., Griebler, C., Konecny-Dupre, L., Martinez, A., Mori, N., Nanni, V., Ogorelec, Ž., Pallares, S., Salussolia, A., Sacco, M., Stoch, F., Vaccarelli, I., Zagmajster, M., Zittra, C., Meierhofer, M.B., Sanchez-Fernandez, D., & Malard, F., 2024, Perspectives and pitfalls in preserving subterranean biodiversity through protected areas. npj Biodiversity 3, 2.

Mata da Rocha Melo, L., Ferreira, R.L., & Souza Silva, M., 2025, A review of the factors influencing invertebrate community structure in subterranean habitats. Community Ecology https://doi.org/10.1007/s42974-025-00243-8

Nicolosi, G., & Gerovasileiou, V., 2024, Towards invasion ecology for subterranean ecosystems. Biodiversity and Conservation 33:1561–1569.

Nicolosi, G., Mammol, S., Verbrugge, L., & Isaia, M., 2023, Aliens in caves: the global dimension of biological invasions in subterranean ecosystems. Biological Reviews 98: 849–867.

Niemiller, M.L., Zigler, K., Curtis, A., Trapeni, C.M., Slay, M.E., Culver, D.C., Hutchins, B.T., & Kendall Niemiller, K.D., 2025, Out of sight and out of mind? The conservation status of subterranean biodiversity in the United States and Canada. Biodiversity and Conservation 34: 2851–2882.

Pipan, T., López, H., Oromí, P., Polakd, S., & Culver, D.C., 2010, Temperature variation and the presence of troglobionts in terrestrial shallow subterranean habitats. Journal of Natural History 45: 253–273.

Poulson, T.L., & White, W.B., 1969, The cave environment. Science 165: 971–981.

Raschmanová, N., Šustr, V., Kováč, L., Parimuchová, A., & Devette, M., 2018, Testing the climatic variability hypothesis in edaphic and subterranean Collembola (Hexapoda). Journal of Thermal Biology 78: 391–400.

Rastetter, E.B, Ohman, M.D., Elliot, K.J., Rehaje, J.S., Rivera-Monroy, V.H., Boucek, R.E., Castañeda-Moya, E., Danielson, T.M., Gough, L., Groffman, P.M., Jackson, C.R., Miniat, C.F., & Shaver, G.R., 2021, Time lags: insights from the U.S. Long Term Ecological Research Network. Ecosphere 12, e03431.

Reinke, B.A., Millar, D.A.W., & Janzen, F.J., 2019, What have long-term field studies taught us about population dynamics. Annual Review of Ecology, Evolution, and Systematics 50: 11.1–11.18.

Saccò, M., Mammola, S., Altermatt, F., Alther, R., Bolpagni, R., Brancelj, A., Brankovits, D., Fišer, C., Gerovasileiou, V., Griebler, C., Guareschi, S., Hose, G.C., Korbel, K., Lictevout, E., Malard, F., Martínez, A., Niemiller, M.L., Robertson, A., Tanalgo, K.C., Bichuette, M.E., Borko, S., Brad, T., Campbell, M.A., Cardoso, P., Celico, F., Cooper, S.J.B., Culver, D.C., Di Lorenzo, T., Galassi, D.M.P., Guzik, M.T., Hartland, A., Humphreys, W.F., Ferreira, R.L., Lunghi E., Nizzoli D., Perina G., Raghavan R., Richards Z., Reboleira A.S.P.S., Rohde M.M., Sánchez Fernández, D., Schmidt, S.I., van der Heyde, M., Weaver, L., White, N.E., Zagmajster, M., Hogg, I., Ruhi, A., Gagnon, M.M., Allentoft, M.E., & Reinecke, R., 2023, Groundwater is a hidden global keystone ecosystem. Global Change Biology 30, e17066

Sánchez-Fernández, D., Rizzo, V., Bourdeau, C., Cieslak, A., Comas, J., Faille, A., Fresneda, J., Lleopart, E., Millán, A., Montes, A., Pallarés, S., & Ribera, I., 2018, The deep subterranean environment as a potential model system in ecological, biogeographical and evolutionary research. Subterranean Biology 25: 1–7.

Sánchez-Fernández, D., Galassi, D.M.P., Wynne, J.J., Cardoso, P., & Mammol, S., 2021, Don't forget subterranean ecosystems in climate change agendas. Nature Climate Change 11: 458–459.

Silveira, F.A.O., 2025, Seven ways to prevent biomism. Ambio 54: 1491–1495.

Simon, K.S., Pipan, T., & Culver, D.C., 2007, A conceptual model of the flow and distribution of organic carbon in caves. Journal of Cave and Karst Studies 69: 279–284.

Sket, B., 2008, Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42: 1549–1563.

Stroud, J.T, & Ratcliff, W.C., 2025, Long-term studies provide unique insights into evolution. Nature 639: 589–601.

Trajano, E., 2000, Cave faunas in the Atlantic tropical rain forest: Composition, ecology, and conservation. Biotropica 32: 882–893.

Vaccarelli, I., Colado, R., Pallarés, S., Galassi, D.M.P., Sanchez-Fernandez, D., Di Cicco, M., Meiherhofer, M., Piano, E., Di Lorenzo, T. & Mammola, S., 2023, A global meta-analysis reveals multilevel and context-dependent effects of climate change on subterranean ecosystems. One Earth 6: 1–13.

White, W.B., Culver, D.C., & Pipan, T., 2019, Encyclopedia of Caves, 3rd ed. Amsterdam, The Netherlands: Elsevier Press, pp. 1118–1127.